

The University of Chicago

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GROWTH AND MINERAL
NUTRITION OF BEAN

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

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By

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EFFECTS OF LIGHT QUALITY ON GROWTH AND MINERAL NUTRITION OF BEAN

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 546

LAWRENCE M. ROHRBAUGH

(WITH NINE FIGURES)

Introduction

The effect of light quality on the growth of plants has been reviewed by BURKHOLDER (1) and by POPP and BROWN (17). Various types of light sources and filters have been used, but in most cases the spectral regions incident to the plant were not known except as to their effect on the eye. This was especially true in the earlier experiments. Likewise the intensities of the light used have not been well controlled, and it is difficult to separate the effects of differing light quality from the effects of differing light quantity.

The use of fluorescent lamps as a source of light for growing plants has been reported by NAYLOR and GERNER (14), NAYLOR (13), and FLINT and MORELAND (4). Use of the different colors of fluorescent lamps which are available was suggested by NAYLOR (13) for the determination of some of the effects of light quality on plant growth. While most of these colored lamps emit some light in nearly all parts of the visible spectrum, the fact that most of the energy is emitted within comparatively narrow regions of the spectrum makes it possible to use filters with them which will absorb all the light from certain spectral regions without losing much of the radiated energy. Because of their efficiency in this respect, fluorescent lamps were chosen as a favorable source of light for the experiments on the effects of light quality reported in this paper.

Material and methods

LIGHT SOURCES AND FILTERS

Six 30-watt, 36-inch, fluorescent tubes were installed in metal reflectors as described by NAYLOR (13). Curtains made of double-thickness black sateen cloth were placed around each of the reflectors and extended almost to the floor. The inside of these curtains was painted white in order to increase and better equalize the light intensity at all points under the reflector. The flanges of the reflectors were fitted with sheet metal strips so that gelatin filters could be inserted in them to cover the entire lamp.

To eliminate certain parts of the spectrum, dyed gelatin filters were used. WHITMORE (27) has determined the transmission curves for many dyes, and three dyes were selected from this group which had regions of transmission and absorption suitable for these experiments and which would not fade under the lights. These were orange G, naphthol yellow, and pontamine fast turquoise blue.

The gelatin filters were prepared in the following manner. Panes of window glass which had been cut to fit the reflectors (20×46 inches) were washed and dried. A pane was then placed on a table and carefully leveled with a spirit level. A gelatin mixture was prepared by heating about 75 gm. of clear gelatin and 30 gm. of sorbitol in 800 ml. of water on a steambath. This approximates 130 gm. of gelatin and 50 gm. of sorbitol per

square meter of surface covered. While this mixture was still warm, about 300 ml. of water containing the desired amount of dissolved dye was added and the entire mixture stirred. The amounts of gelatin, sorbitol, or water used are not critical. About 1100 ml. of the liquid worked very well in covering the 20×46 inches glass pane. The hot dyed gelatin mixture was cooled to about 60° C. and then poured on the glass plate. A glass rod was used to spread the gelatin to the sides and corners of the glass. The gelatin was filtered through several thicknesses of cheesecloth as it was poured in order to eliminate as many bubbles as possible. Any bubbles found on the poured filters were removed by touching them with the glass rod. While surface tension will prevent the melted gelatin from running over the edges of the glass if it does not become too deep and if strong currents are avoided, it was found that rubbing a piece of paraffin along the edges of the glass made accidents less frequent at this point. The filters should not be moved until thoroughly cooled. When dry, they were inserted in the reflectors, with the gelatin side down.

The orange G filter was prepared to contain 4 gm. of orange G (Dupont) per square meter. This filter transmitted no light of wave length shorter than 5300 Å. The naphthol yellow filter contained 5 gm. of naphthol yellow (Coleman and Bell) per square meter and transmitted no light of wave length shorter than 4850 Å. Two turquoise blue filters were used. One contained 4 gm. of pontamine fast turquoise blue (Dupont) per square meter and transmitted no light with wave length greater than 5750 Å and only 0.5 per cent of the incident light at 5650 Å. The other contained 2 gm. of the dye per square meter and transmitted some light of longer wave length. The

transmission curves for these filters were determined with a Keuffel and Esser spectrophotometer (fig. 1). The quality of light reaching the plants is indicated by the spectrograms in figure 2. These spectrograms were made by using a small spectroscope with a camera. The film used was Eastman Panatomic X, and the time of exposure was equal in all cases.

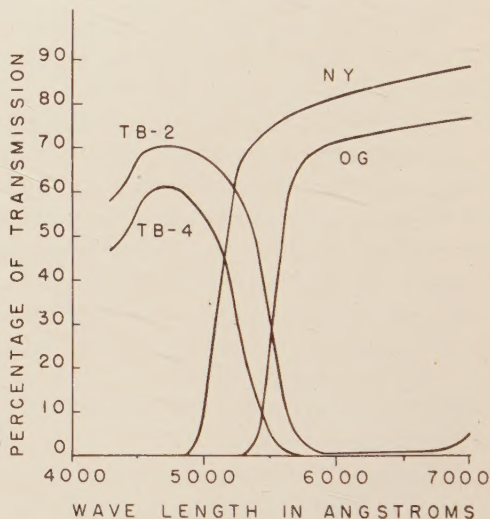


FIG. 1.—Transmission of light by dyed gelatin filters: TB-2, turquoise blue, 2 gm. per sq. m.; TB-4, turquoise blue, 4 gm. per sq. cm.; NY, naphthol yellow, 5 gm. per sq. cm.; OG, orange G, 4 gm. per sq. cm.

The spectroscope was placed at varying distances from the different lamps, so that the incident energy at the spectroscope was equal for all the lamps. Because of the nature of the spectroscope, it is doubtful whether bands in the ultraviolet would have reached the film, even if they had been present in the incident light. Each of the lamps was fitted either with a gelatin filter or with a pane of window glass at the time the spectrograms were made. These spectrograms present a much more accurate measure of the quality of light emitted by the various colors of fluorescent tubes than is pre-

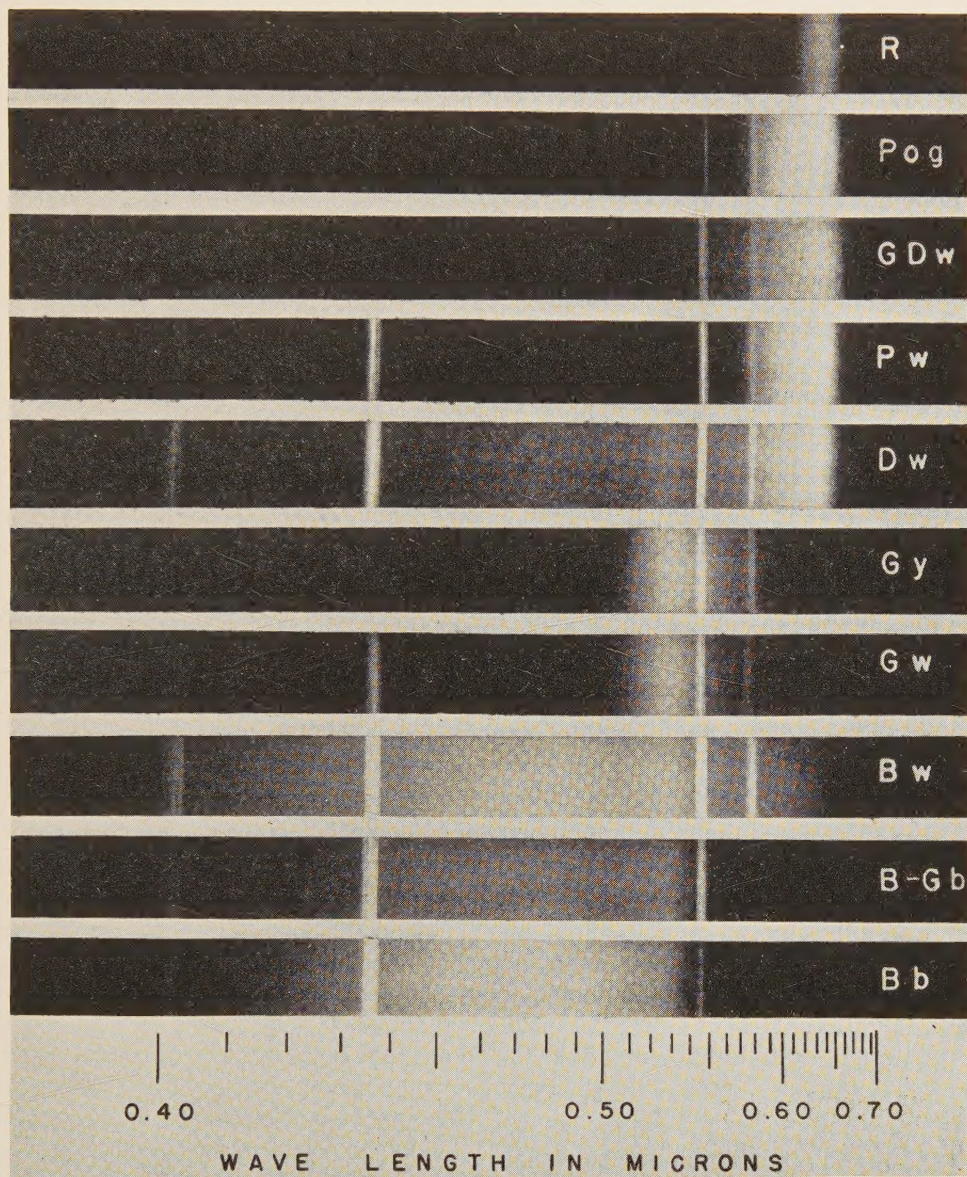


FIG. 2.—Spectrograms of light emitted by different colored fluorescent lamps with window glass and dyed gelatin filters: R, red without filter; P o g, pink with orange G filter; G D w, gold with window glass; P w, pink with window glass; D w, daylight (fluorescent) with window glass; G y, green with naphthol yellow filter; G w, green with window glass; B w, blue with window glass; B-G b, blue and green with turquoise blue filter; B b, blue with turquoise blue filter.

sented in the curves prepared by the manufacturer. Most of the energy is emitted in a series of very narrow bands of the spectrum and not in a broad band with gradual decreasing energy at either end, as represented by the manufacturer's curves.

MEASUREMENT OF RADIANT ENERGY

The total energy incident to a surface at the level of the plants was measured with a thermopile which had been calibrated with a standard lamp obtained from the United States Bureau of Standards,¹ and the distance from the lamps to the plants was varied so that the incident energy was approximately equal in all cases. The thermopile was connected with a balancing circuit, and a galvanometer was used as a null point indicator. A microammeter in the balancing circuit measured the amount of current needed to balance the thermopile current and provided a means of comparison with the standard lamp. The light intensities were also measured with a Weston foot-candle meter. As the plants grew it became more difficult to maintain equal incident energy values, since the plants no longer presented a single plane of surfaces for the reception of light but rather a series of surfaces from the top of the plant down almost to the pot level. Equal energies at the pot level or at the top of the plant would be meaningless since the light sources were at widely varying distances. Therefore an attempt was made to estimate the average level of the plant surfaces, and the distances of the lamps were adjusted to produce equal incident energy at those levels.

¹ The thermopile was arranged and calibrated by Mr. R. A. WHITMORE, who also assisted in some of the measurements of light energy.

CULTURE OF PLANTS

Red kidney bean (*Phaseolus vulgaris*) plants were grown in quartz sand in glazed crocks. Five seeds were planted in each crock, and three rows of seven or eight crocks each were placed under each reflector. After development of the primary leaves, the plants were thinned to two uniform seedlings per crock. The positions of the three rows were changed each week in order to minimize the effects of different light intensities which may have existed between the center and outside positions.

Although the seeds were treated with dry Semesan before planting, many of the seedlings were lost because of infection with damping-off fungus. In the first two experiments the infected seedlings were replaced by transplanting ones of the same age which had been germinated in sand. In the later experiments, the crocks were kept in a dark-room in which the temperature was about 80° F. and the humidity low for several days after the seeds were planted. As soon as the first seedlings appeared above the surface of the sand, all the crocks were placed under the lights. This procedure apparently prevented activity of the fungus.

The plants were grown in a basement room, where the temperature was rather constant from day to day but varied from about 68° F. in winter to about 75° F. in summer. The temperature under the lamps was somewhat higher than this and not entirely the same under the different lamps. Thus on May 5 the temperatures under the various lamps were: pink with filter, 27.8° C.; gold, 28.9° C.; pink without filter, 27.0° C.; daylight, 26.8° C.; green with filter, 27.8° C.; green without filter, 27.8° C.; blue without filter, 27.1° C.; blue-green

with filter, 29.3° C.; and blue with filter, 28.4° C.

The plants were grown on cycles of 20 hours of light and 4 hours of dark in all the experiments. The composition of the nutrient solutions used is given in table 1. These solutions were applied as often as required to keep the top of the sand moist.

MEASUREMENTS AND CHEMICAL ANALYSIS

When harvested, the lengths of the hypocotyl and stem, the number of inter-

complete nutrient solution in experiments 2 and 3. Semi-micro methods were used.

The dried tissue was ground in a micro-Wiley mill until it passed a 50-mesh screen. The powdered material was then dried to constant weight. Duplicate 0.5-gm. samples were weighed out and ashed in a muffle at 600° C. for 2 hours. After the weight of the ash had been determined, it was dissolved in 1:5 HCl, transferred to a 100-ml. volumetric flask, and made to volume with water. Aliquots were then taken for the deter-

TABLE 1
COMPOSITION OF NUTRIENT SOLUTIONS*

NUTRIENT SOLUTION	AMOUNT OF M/2 STOCK SOLUTION PER LITER OF SOLUTION (ML.)					
	Ca(NO ₃) ₂	KH ₂ PO ₄	NaH ₂ PO ₄	KCl	MgSO ₄	Na ₂ SO ₄
Complete.....	12	3.0		6.0	4.0	
Low K.....	12	1.0	2.0		4.0	
Low P.....	12	0.025		8.975	4.0	
Minus P.....	12			9.0	4.0	
Low Mg.....	12	3.0		6.0	0.4	3.6
Minus Mg.....	12	3.0		6.0		4.0

* Micronutrients were also added to make the following concentrations: 0.5 p.p.m. of boron as Na₂B₄O₇, 0.5 p.p.m. of zinc as ZnCl₂, 0.5 p.p.m. of iron as ferric citrate, and 0.125 p.p.m. of copper as CuCl₂.

nodes, the number of flower buds, and the fresh weight of leaves and stems were determined. The roots were washed in salt water to free them of sand. The plants were dried at 80° C. in a forced-draft gas oven, and the dry weights of leaves, stems, and roots were determined. In later experiments the lengths of the first and second internodes and the average area of the leaflets were determined. The area of from thirty to eighty leaflets was measured by the photoelectric device described by MITCHELL (12). No obviously juvenile leaves were included in these measurements.

The amounts of total ash, calcium, magnesium, potassium, and phosphorus were determined for the plants grown on

mination of calcium, magnesium, potassium, and phosphorus.

Calcium was precipitated as the oxalate, as described by KRAMER and TISDALL (9), and separated by centrifugation. Determination was made by titration with 0.01 normal potassium permanganate, using an electrometric titration assembly similar to that described by KASSNER, HUNZE, and CHATFIELD (8).

Magnesium was precipitated and separated from the supernatant liquid from the calcium determination according to the method of KRAMER and TISDALL (9), as modified by HAMMETT and ADAMS (6), and was determined colorimetrically as described by WALL (23). The method of separation of calcium and magnesium

described by WALL was found to be satisfactory for the calcium, but it was not reliable for the small quantities of magnesium present in these tissues.

Potassium was precipitated as the cobaltinitrite and determination made colorimetrically on the basis of the color produced by the reaction of cobalt with Nitroso-R salt as described by SIDERIS (21).

Phosphorus was determined colorimetrically by the method described by WALL (23). All colorimetric determinations were made with a Keuffel and Esser spectrophotometer.

Experimentation

Red, gold, pink, daylight, green, and blue fluorescent tubes were used in experiment 1. Each reflector was fitted with different colored tubes. No window glass or filters were used under the reflectors in this experiment. The incident energy at the level of the plants was 2431 microwatts/sq. cm., or 581×10^{-6} gm. cal./sq. cm./sec. Measured in foot-candles, the intensity varied from 158 under the red to 460 under the gold.

The crocks under each reflector were divided into four groups, receiving complete, low magnesium, low potassium, and low phosphorus nutrient solutions. Because of the damping-off fungus which attacked the hypocotyls of the seedlings, most of the plants had to be replaced with ones transplanted from large germination crocks.

Eight reflectors were used in the second experiment. Two were fitted with pink tubes, two with green, two with blue, one with gold, and one with daylight. Under one set of the pink tubes was placed an orange G filter; under one set of the green tubes was placed a naphthol yellow filter; and under one set of the blue tubes was placed a turquoise blue

filter (4 gm. per sq. m.). Ordinary window glass was placed under all the other reflectors. The lamps were adjusted to give 1750 microwatts/sq. cm., or 418×10^{-6} gm. cal./sq. cm./sec., at the level of the plants. The intensity as measured with the Weston foot-candle meter varied from 270 foot-candles under the pink with filter to 360 foot-candles under the green with filter.

The damping-off fungus again necessitated using transplanted plants in most cases. The plants grown under each reflector were divided into three groups, one being watered with complete nutrient solution, one with low phosphorus solution, and one with minus phosphorus solution.

For experiment 3 the eight reflectors used in experiment 2 were again employed, and in addition a ninth reflector was used which was fitted with four blue tubes and two green tubes and a gelatin filter made with 2 gm. of turquoise blue per sq. m. The light intensities were adjusted as in experiment 2. Twenty-four crocks were placed under each reflector. These were divided into four groups of six crocks each. Three of these groups were given the three different levels of phosphorus nutrition used in experiment 2. The crocks of the fourth group were watered with complete nutrient solution, except for iron, which was supplied in amounts varying from none to 5 p.p.m.

In experiment 4 the nine reflectors of experiment 3 were again used with the same tubes and filters. The incident energy at the level of the plants in this experiment was 1314 microwatts/sq. cm., or 314×10^{-6} gm. cal./sq. cm./sec. Two-thirds of the plants were watered with complete nutrient solution and one-third with minus magnesium solution.

The same lamps and filters were again used in experiment 5. Some of the re-

flectors were repainted before beginning this experiment in order to raise the intensity of the light. The incident energy at the level of the plants was 1705 micro-watts/sq. cm., or 408×10^{-6} gm. cal./sq. cm./sec. The plants were divided into two groups, which were watered with complete and minus magnesium nutrient solutions as in experiment 4.

Results

The plants grown in experiment 4 were harvested 31 days after planting, which was soon after the first flower buds became visible. In the other experiments the plants were harvested 39–51 days after planting, which was soon after flowering had started.

In all cases except experiment 4, visible flower buds appeared on plants grown under green light earlier than on plants grown under any of the other lamps. In experiment 4 flower buds appeared at approximately the same time on plants grown under all the lamps except the blue without the filter. Plants grown under this lamp did not have visible buds at the time of harvesting. Many of the flower buds which appeared on the plants grown under the green lights abscised before the plants were harvested, so that the number of flower buds present at the time the plants were harvested was sometimes greater on the plants grown under the daylight and blue tubes without the filter.

The plants grown under the red tubes in experiment 1 were very unthrifty. They had short internodes and small and wrinkled leaflets. Since about one-half of these plants died before harvesting, it is possible that some other factor may have resulted in their poor growth, and comparison of these plants with those grown under the other lamps may not be valid.

Many of the plants grown under the

gold, pink with filter, and green with filter became chlorotic toward the tops. Some of the younger leaves appeared entirely lacking in both chlorophyll and carotenoid pigments. This condition was not noticed in any of the plants which received energy from the blue end of the spectrum. The chlorosis was apparently unrelated to the amount of iron supplied to the plants, because it appeared equally severe in the plants given the different concentrations of iron in experiment 3.

Table 2 summarizes the data obtained from experiment 5. Some of the data for the other experiments are shown in figures 3–7.

The lengths of the hypocotyls and internodes of plants grown under the different lamps are shown in figure 3. The shortest hypocotyls and first internodes were found on plants grown under daylight and blue tubes without filters other than window glass. The spectrograms of figure 2 indicate that both of these lamps emit light from nearly all regions of the visible spectrum, but that the percentage of the total energy emitted in the orange-red region is very low in the blue tubes while rather high in the daylight tubes. The effect on the growth of the plants was much the same under the two lamps.

Plants grown under the blue tubes with the turquoise blue filter received no light with wave length longer than 5800 Å and very little with wave length longer than 5600 Å. Plants grown under this lamp produced longer hypocotyls and first internodes than were produced under any of the other lamps. The green tubes emit considerable energy in the blue line and some in the violet line of the mercury arc, but emit very little in the region above 6000 Å. Plants grown under these tubes produced much shorter hypocotyls and first internodes than were

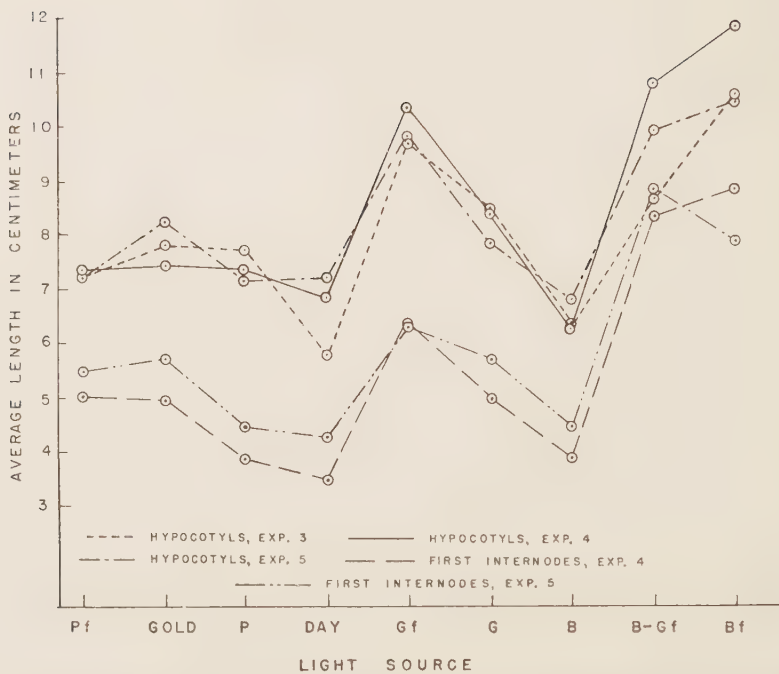


FIG. 3.—Average length of hypocotyls and first internodes of bean plants grown under different colored fluorescent lamps: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

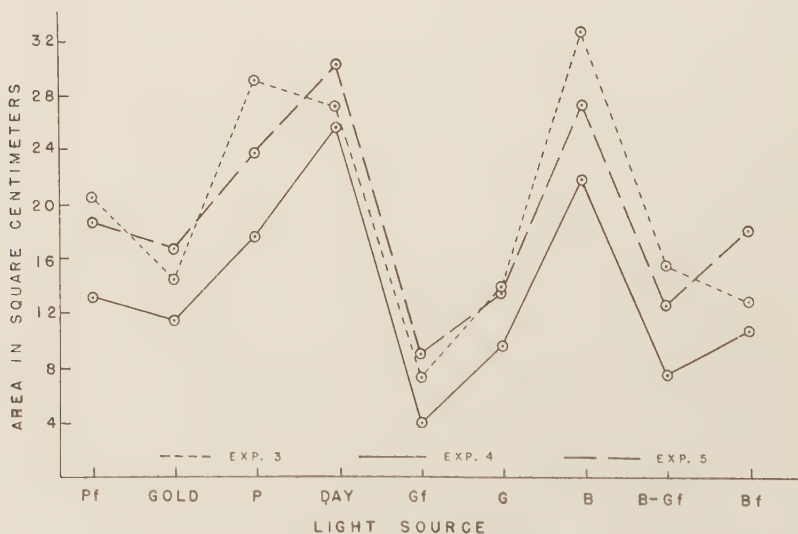


FIG. 4.—Average area of leaflets of bean plants grown under different colored fluorescent lamps: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

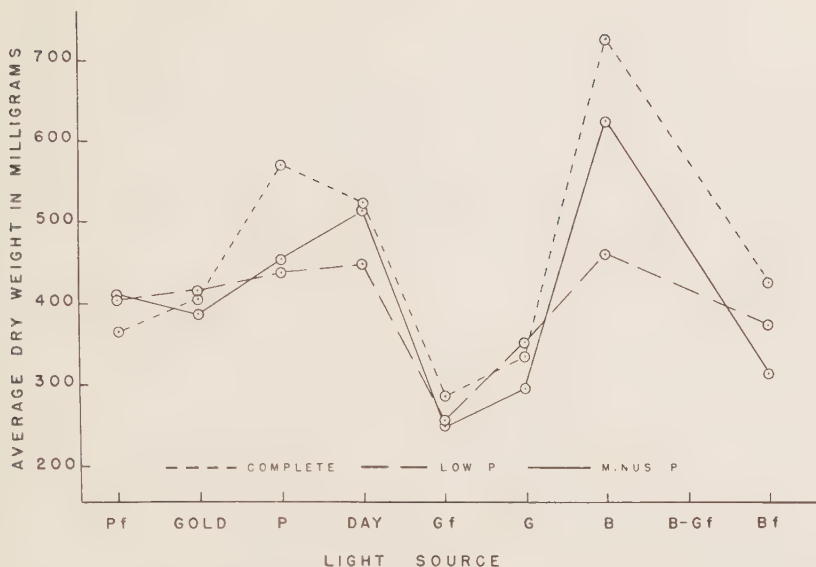


FIG. 5.—Average dry weights of bean plants grown on complete, low phosphorus, and minus phosphorus solutions under different colored fluorescent lamps; experiment 2: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

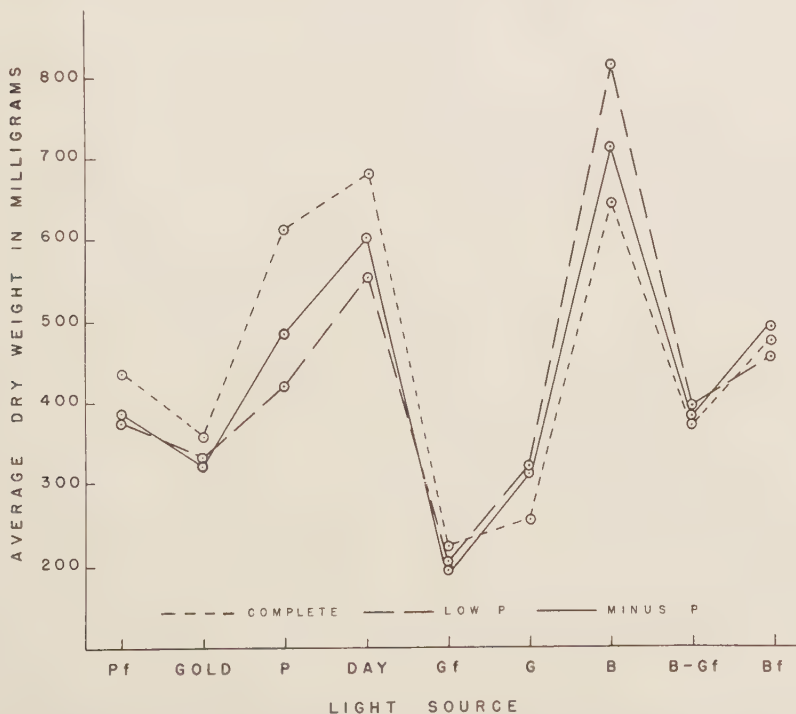


FIG. 6.—Average dry weights of bean plants grown on complete, low phosphorus, and minus phosphorus solutions under different colored fluorescent lamps; experiment 3: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

produced under the blue tubes with the filter but longer ones than were produced under the blue without the filter or under the gold, daylight, or pink tubes. In these cases red light was apparently much more effective in inhibiting growth in length of plants than was blue light. This was also indicated by the very short stems produced under the red tubes in experiment 1. The average length of the

naphthol yellow filter, the lengths of the hypocotyls and first internodes became almost as great as were obtained under the blue tubes with the filter. Also the hypocotyls and first internodes produced under the pink tubes with the orange G filter and under the gold tubes—neither of which emitted light of shorter wave length than about 4900 Å and very little shorter than 5200 Å—were longer than

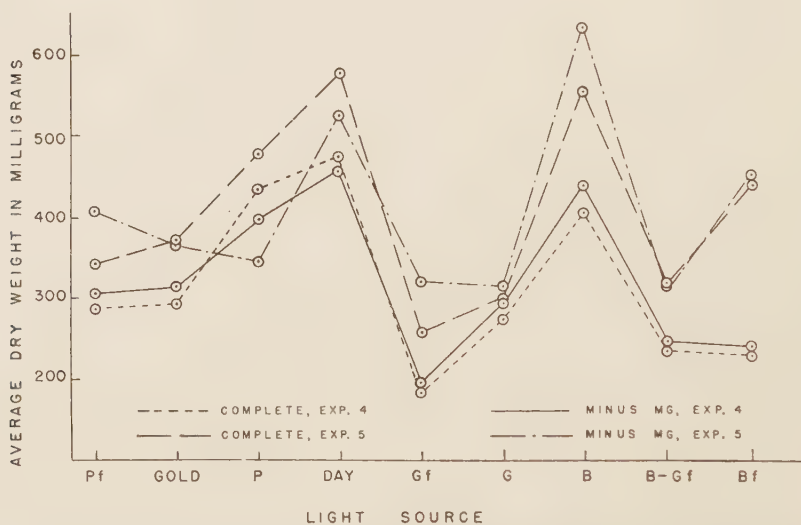


FIG. 7.—Average dry weights of bean plants grown on complete and minus magnesium solutions under different colored fluorescent lamps: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

internodes produced by these plants was 1.9 cm., while the average length of the internodes produced by the plants grown under the gold tubes in the same experiment was 4.3 cm., and plants grown under the other lights produced still longer internodes. About half the plants grown under the red tubes had died by the end of the experiment, however, and it is possible that some condition other than red light caused the short stems.

When the blue and violet light of the green tubes was absorbed by use of the

those produced by plants subjected to the more balanced radiations of the daylight, blue, or pink tubes without filters. In these cases the blue end of the spectrum may have been somewhat effective in inhibiting stem elongation.

The lengths of the upper internodes did not seem to be affected by the different lamps in the same way as were the hypocotyls and lower internodes. Plants with long hypocotyls and first internodes tended to have shorter upper internodes than did those which had shorter hypocotyls and first internodes.

The average areas of the leaflets of the plants grown under the different lamps are shown in figure 4. The effect of the light quality on leaf area seems to be somewhat the opposite of the effect on elongation of stems. The largest leaves developed under the well-balanced light of the daylight and blue tubes without

not measured. They were probably smaller than those produced under any of the other lamps during that experiment. As already mentioned, it may not be safe to draw conclusions regarding the plants grown under the red tubes because of their very poor growth. But the leaf areas of the plants grown under the red

TABLE 2

NUMBER OF FLOWER BUDS, AREA OF LEAFLETS, LENGTHS, WEIGHTS, AND TOP/ROOT RATIOS OF BEAN PLANTS GROWN WITH COMPLETE AND MINUS MAGNESIUM NUTRITION UNDER DIFFERENT CONDITIONS OF LIGHT QUALITY: EXPERIMENT 5

LIGHT	NUTRIENT SOLUTION	NO. OF PLANTS	AVERAGE NO. OF FLOWER BUDS	AVERAGE AREA OF LEAFLETS (SQ. CM.)	AVERAGE LENGTHS					AVERAGE WEIGHTS PER PLANT					TOP/ROOT RATIO
					HYPOCOTYLS (CM.)	STEMS (CM.)	FIRST INTER-NODES (CM.)	SECOND INTER-NODES (CM.)	ALL INTER-NODES (CM.)	LEAVES		STEMS		ROOTS	
										FRESH (GM.)	DRY (GM.)	FRESH (GM.)	DRY (GM.)	DRY (GM.)	
Pf*	Complete -Mg	28	0.18	18.7	7.29	36.1	5.55	5.70	6.10	2.21	0.166	1.46	0.117	0.062	4.56
		13	0.23		6.96	39.8	5.77	6.23	6.64	2.77	0.212	1.55	0.129	0.069	4.94
Gold.	Complete -Mg	25	0.80	16.9	8.30	41.6	5.80	5.96	6.80	2.44	0.182	1.56	0.128	0.064	4.84
		15	0.47		8.03	40.5	5.27	6.07	6.76	2.59	0.186	1.53	0.123	0.059	5.24
P....	Complete -Mg	25	0.44	23.9	7.20	42.1	4.54	5.60	7.11	3.29	0.260	1.67	0.146	0.072	5.64
		15	0.20		7.03	40.5	4.80	5.80	6.99	2.91	0.231	1.56	0.135	0.080	3.33
Day.	Complete -Mg	23	1.04	30.3	7.28	41.0	4.26	5.83	6.93	3.88	0.344	1.70	0.160	0.075	6.72
		16	0.56		7.44	39.3	3.84	5.37	6.69	3.44	0.290	1.76	0.159	0.076	5.91
Gf...	Complete -Mg	25	2.16	9.0	9.90	32.2	6.34	6.48	5.87	1.27	0.107	1.40	0.102	0.050	4.18
		14	3.50		9.57	33.4	6.75	6.96	6.24	1.66	0.141	1.49	0.112	0.067	3.78
G....	Complete -Mg	25	2.96	13.4	7.86	36.4	5.74	6.20	6.32	1.85	0.140	1.30	0.104	0.053	4.60
		12	2.58		8.17	35.5	5.54	5.96	6.09	1.86	0.143	1.33	0.106	0.063	3.95
B....	Complete -Mg	20	0.50	27.2	6.83	43.4	4.40	6.35	7.11	3.64	0.331	1.73	0.155	0.067	7.25
		14	0.71		6.46	42.9	4.61	6.68	7.23	4.38	0.385	1.74	0.164	0.082	6.70
B-Gf.	Complete -Mg	25	0.04	12.5	9.94	42.1	8.88	7.98	7.41	1.56	0.134	1.67	0.120	0.060	4.23
		13	0.00		9.96	38.8	8.50	7.73	7.11	1.52	0.131	1.66	0.122	0.058	4.36
Bf...	Complete -Mg	22	1.23	18.1	10.48	49.1	7.89	9.41	8.86	2.39	0.212	1.97	0.165	0.060	6.28
		12	1.17		10.21	50.1	7.92	8.88	8.71	2.37	0.218	2.00	0.163	0.068	5.60

* Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight fluorescent without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue-green with filter; and Bf, blue with filter.

filters. The smallest developed under the green tubes with the filter. If only those lights are considered which emitted quite narrow regions of the spectrum (pink with filter, gold, green with filter, blue-green with filter, and blue with filter), then the largest leaves developed under the red end of the spectrum, the next largest under the blue end, and the smallest under the green region. The areas of the leaves of the plants grown under the red tubes in experiment 1 were

tubes appear to be an exception to the general tendency for larger leaves under the red end of the spectrum.

No detectable deficiency symptoms developed in the plants grown on low or minus phosphorus or on minus magnesium solutions during these experiments. A comparison of the dry weights produced by the plants grown under the different conditions of nutrition and light quality is shown in figures 5-7. While in many cases the dry weight produced by

plants grown on complete nutrient solution was greater than that produced by plants grown on the solutions deficient in phosphorus or magnesium, in many cases the opposite condition was found. It is probable that the number of plants

analyses are shown in tables 3 and 4. While the amount of ash, expressed as percentage dry weight, did vary somewhat among plants grown under the different lights, the direction of variance was not the same in the two experiments

TABLE 3

AMOUNT OF TOTAL ASH, CALCIUM, MAGNESIUM, POTASSIUM, AND PHOSPHORUS IN LEAVES, STEMS AND TOPS OF BEAN PLANTS GROWN UNDER DIFFERENT CONDITIONS OF LIGHT QUALITY: EXPERIMENT 2

PLANT TISSUE	LIGHT	ASH		CALCIUM		MAGNESIUM		POTASSIUM		PHOSPHORUS	
		PER-CENTAGE DRY WEIGHT	MILLI-GRAMS PER PLANT	PER-CENTAGE DRY ASH	PER-CENTAGE DRY WEIGHT	PER-CENTAGE DRY ASH	PER-CENTAGE DRY WEIGHT	PER-CENTAGE DRY ASH	PER-CENTAGE DRY WEIGHT	PER-CENTAGE DRY ASH	PER-CENTAGE DRY WEIGHT
Stems	Pf*.....	12.8	13.1	15.8	2.03	2.03	0.26	38.2	4.89	5.19	0.67
	Gold.....	16.6	16.9	14.5	2.11	1.79	0.26	41.3	6.01	5.66	0.82
	P.....	13.6	19.8	12.1	1.64	1.09	0.15	42.0	5.70	5.04	0.68
	Day.....	12.2	16.5	13.1	1.60	2.11	0.26	42.1	5.15	4.99	0.61
	Gf.....	14.0	13.6	13.6	1.91	2.07	0.29	39.2	5.50	7.21	1.01
	G.....	13.8	12.8	13.2	1.81	1.85	0.25	44.3	6.10	5.67	0.78
	B.....	11.3	17.7	10.4	1.17	1.38	0.16	46.5	5.24	5.15	0.58
	Bf.....	12.0	15.2	11.0	1.32	2.41	0.29	43.5	5.22	5.90	0.71
Leaves	Pf.....	16.0	29.4	12.1	1.93	3.20	0.51	37.9	6.05	6.63	1.07
	Gold.....	17.5	34.9	12.5	2.18	2.75	0.48	41.0	7.16	6.90	1.21
	P.....	17.1	57.3	15.7	2.68	2.86	0.49	41.8	7.13	5.46	0.93
	Day.....	14.8	42.6	14.6	2.15	3.32	0.49	43.5	6.42	5.76	0.85
	Gf.....	16.7	20.8	12.7	2.12	3.30	0.55	41.8	6.97	6.84	1.14
	G.....	15.9	28.0	12.6	2.00	3.44	0.55	48.7	7.73	6.65	1.06
	B.....	14.8	65.3	15.7	2.32	3.51	0.52	41.1	6.06	5.30	0.78
	Bf.....	14.6	32.7	14.3	2.10	4.01	0.59	40.0	5.87	5.90	0.86
Tops	Pf.....	14.8	42.5	13.3	1.97	2.83	0.42	38.0	5.64	6.27	0.93
	Gold.....	16.4	51.8	13.2	2.16	2.25	0.37	41.1	6.74	6.52	1.07
	P.....	16.0	77.2	14.7	2.36	2.44	0.39	41.9	6.70	5.31	0.85
	Day.....	14.0	59.1	14.1	1.97	3.01	0.42	43.1	6.01	5.52	0.77
	Gf.....	15.5	34.5	13.0	2.02	2.77	0.43	41.6	6.30	6.96	1.08
	G.....	15.2	40.8	12.7	1.93	2.97	0.45	47.3	7.16	6.40	0.97
	B.....	13.8	83.0	14.6	2.02	3.11	0.43	42.3	5.85	5.27	0.73
	Bf.....	13.7	47.9	13.3	1.82	3.51	0.48	41.3	5.64	5.90	0.81

* See footnote to table 2 for explanation of abbreviations.

used was too small for any of these differences to be considered significant. Failure to obtain typical deficiency symptoms probably resulted from the storage of the necessary elements in the seed and from the low light intensities used.

Mineral analyses were made on the leaves and stems of the plants grown on complete nutrient solutions in experiments 2 and 3. The results of these

in which mineral analyses were made. It is probable that these differences are of little significance.

No consistent differences were found in the amounts of potassium present under the different conditions of light quality, except that the highest values for the leaves and for the entire tops were found in plants grown under the green tubes without the filter, and the

highest values for the stems were found under the blue without the filter.

The amount of calcium in the leaves of plants grown under the different lamps (fig. 8) followed an order similar to that for dry weight production and leaf area

fect of light quality on the calcium content of the stems seemed to be the opposite of the effect noted for the leaves. When the calcium content of the leaves was high the content of the stems was low, and vice versa. If only those lamps

TABLE 4

AMOUNT OF TOTAL ASH, CALCIUM, MAGNESIUM, POTASSIUM, AND PHOSPHORUS IN LEAVES, STEMS AND TOPS OF BEAN PLANTS GROWN UNDER DIFFERENT CONDITIONS OF LIGHT QUALITY: EXPERIMENT 3

PLANT TISSUE	LIGHT	ASH		CALCIUM		MAGNESIUM		POTASSIUM		PHOSPHORUS	
		PER-CENTAGE DRY WEIGHT	MILLI-GRAMS PER PLANT	PER-CENTAGE ASH	PER-CENTAGE DRY WEIGHT	PER-CENTAGE ASH	PER-CENTAGE DRY WEIGHT	PER-CENTAGE ASH	PER-CENTAGE DRY WEIGHT	PER-CENTAGE ASH	PER-CENTAGE DRY WEIGHT
Stems	Pf*.....	14.0	18.1	14.2	1.99	1.70	0.24	41.2	5.77	5.28	0.74
	Gold.....	14.7	16.3	13.2	1.94	1.85	0.27	43.6	6.41	5.34	0.79
	P.....	15.1	26.4	11.2	1.68	1.06	0.16	36.0	5.42	4.07	0.61
	Day.....	14.3	24.7	11.1	1.58	1.13	0.16	43.1	6.16	4.08	0.58
	Gf.....	12.6	11.2	12.3	1.54	2.82	0.35	35.4	4.45	8.13	1.02
	G.....	14.6	13.6	11.8	1.72	1.99	0.29	42.1	6.16	5.71	0.84
	B.....	14.3	22.4	9.9	1.41	1.02	0.15	44.9	6.40	4.32	0.62
	B-Gf.....	14.3	16.5	12.3	1.75	1.82	0.26	38.4	5.48	5.54	0.79
	Bf.....	14.7	21.2	11.6	1.70	1.84	0.27	41.4	6.08	5.30	0.78
	Pf.....	18.1	42.6	13.7	2.49	2.75	0.50	36.3	6.58	4.70	0.85
Leaves	Gold.....	17.8	32.4	14.3	2.54	2.91	0.52	36.4	6.48	4.89	0.87
	P.....	17.6	62.7	17.4	3.05	2.64	0.46	33.7	5.92	3.87	0.68
	Day.....	17.5	72.6	18.2	3.18	2.68	0.47	32.1	5.61	3.82	0.67
	Gf.....	17.4	14.5	11.8	2.06	3.37	0.59	36.3	6.32	5.98	1.04
	G.....	17.2	19.6	14.4	2.48	3.19	0.55	37.1	6.38	5.26	0.90
	B.....	17.2	69.7	18.0	3.10	2.65	0.46	31.8	5.47	3.69	0.63
	B-Gf.....	17.9	35.0	15.5	2.76	2.85	0.51	33.8	6.04	4.29	0.77
	Bf.....	17.4	29.6	14.7	2.56	3.00	0.52	34.3	5.96	4.17	0.73
	Pf.....	16.7	60.6	13.9	2.31	2.46	0.41	37.8	6.29	4.86	0.81
	Gold.....	16.6	48.7	13.9	2.31	2.59	0.43	38.8	6.45	5.05	0.84
Tops	P.....	16.7	89.1	15.5	2.60	2.15	0.36	34.4	5.76	3.94	0.66
	Day.....	16.6	97.3	16.4	2.71	2.30	0.38	34.9	5.77	3.93	0.65
	Gf.....	14.9	25.7	12.0	1.79	3.15	0.47	35.9	5.35	6.84	1.02
	G.....	16.0	33.2	13.3	2.14	2.68	0.43	39.2	6.28	5.42	0.87
	B.....	16.4	92.0	16.1	2.63	2.26	0.37	35.0	5.73	3.85	0.63
	B-Gf.....	16.5	51.6	14.4	2.38	2.54	0.42	35.4	5.84	4.60	0.76
	Bf.....	16.2	50.7	13.4	2.16	2.48	0.40	37.3	6.02	4.64	0.75

* See footnote to table 2 for explanation of abbreviations.

and was greatest in those plants receiving energy from most of the visible spectrum and lower when more selected regions of the spectrum were used. Removal of the red end of the spectrum resulted in about the same degree of lowering of the calcium content as did removal of the blue or of both ends. In general, the ef-

are considered which emit light in rather narrow regions of the spectrum (pink with filter, gold, green with filter, blue-green with filter, and blue with filter), there was a decrease in the calcium content of the stems proceeding from the red to the blue end of the visible spectrum. Since the leaves made up the

greater part of the weight of most of the plants, the percentage of calcium in the entire tops was affected more by the content of the leaves than by that of the stems. Therefore the percentage of calcium in the tops followed an order similar to that for the leaves, but the degree of variation was less.

different lamps in the same way as did the amount expressed as percentage of ash.

There was little difference in the amount of magnesium, expressed as percentage of ash, in plants grown under the different lamps. Expressed as percentage dry weight, the amount of mag-

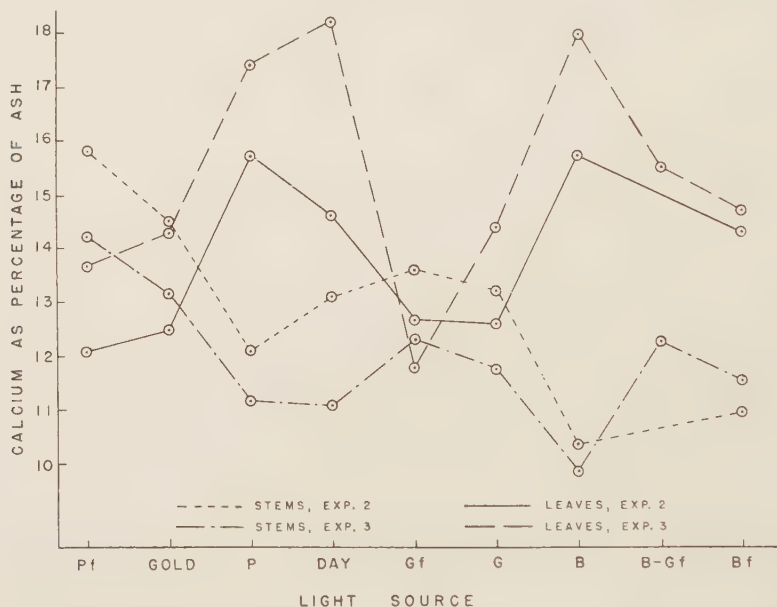


FIG. 8.—Calcium content of bean plants grown under different colored fluorescent lamps: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

The amount of phosphorus, expressed as percentage of ash, is shown in figure 9. It varied under the different lamps oppositely to the variation for calcium. The phosphorus content of those plants grown in the absence of light from the blue end of the spectrum and of those grown without light from the red end was higher than the phosphorus content of plants receiving the more balanced radiation. The phosphorus content was still higher when light from both ends of the spectrum was absent. In general, the amount of phosphorus expressed as percentage dry weight varied under the

nesium in the stems varied in somewhat the same way as did phosphorus. It was highest in plants grown under the green tubes with the filter and lowest in those grown under the pink, daylight, and blue tubes without filters. The variation in the leaves was less marked.

Discussion

There is considerable confusion in the literature regarding the effects of light quality on plant growth. Nearly all the earlier results indicated that the blue end of the spectrum inhibited stem elongation and produced a plant more or

less similar in appearance to those grown in daylight, while plants grown under the red end of the spectrum were long and slender. Most of the experiments were performed with colored glass or colored solutions as filters, and the quality of the light transmitted was not definitely known. Usually no attempt was made to equalize the intensities under the different filters.

same spectral glasses as employed by POPP but included another which transmitted the blue end and absorbed the red end. He used approximately equal intensities under the different filters, measuring them with thermopiles and with a Macbeth illuminometer. *Galinsoga*, sunflower, and *Geum* plants were grown under these filters. Plants grown under the blue filter were somewhat stunted,

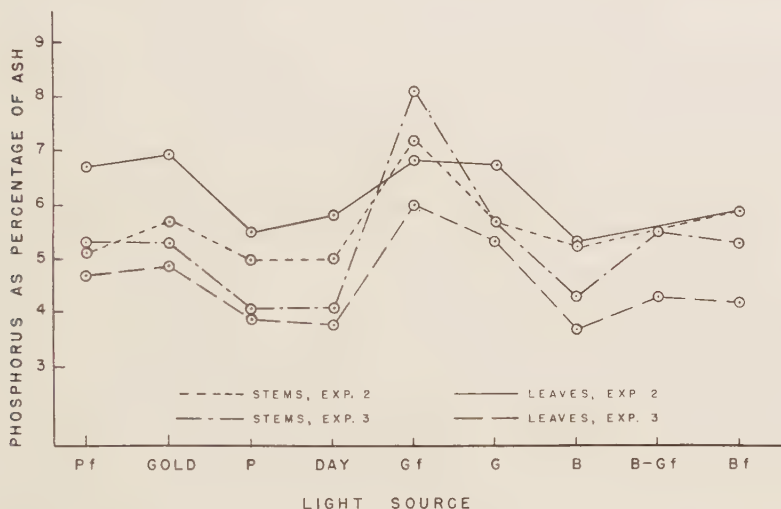


FIG. 9.—Phosphorus content of bean plants grown under different colored fluorescent lamps: Pf, pink with filter; Gold, gold without filter; P, pink without filter; Day, daylight (fluorescent) without filter; Gf, green with filter; G, green without filter; B, blue without filter; B-Gf, blue and green with filter; Bf, blue with filter.

More recently POPP (16), SHIRLEY (20), TEODORESCO (22), and others have reported similar results from experiments which were better controlled, although the light intensities were not fully equated in the experiments reported by POPP and were probably only approximate in many of those of TEODORESCO. POPP used various spectral glasses manufactured by the Corning Glass Company. When progressively greater regions of the blue end of the spectrum were removed, he obtained plants greater in length but containing less dry matter. SHIRLEY (20) used the

having very short internodes but rather sturdy stems. Removal of the blue end of the spectrum resulted in very weak plants, with low dry weight production. Both POPP and SHIRLEY reported that the entire spectrum produced better plants than when any part of the spectrum was removed.

The results of the present experiments agree in part with the results obtained by POPP and by SHIRLEY. Plants getting light from all parts of the visible spectrum had the most normal appearance and produced greater dry weight than did those grown under lamps or filters

which removed part of the spectrum. It was also found that removal of the blue end resulted in plants which had somewhat longer hypocotyls and internodes and which produced less dry weight than did those receiving light from all parts of the spectrum. Curling and sometimes yellowing of the leaves grown in the absence of blue light was reported by POPP and by SHIRLEY, and these conditions were also noted in the present experiments.

If the results obtained under the blue tubes with the filter and under the combination of blue and green tubes with the filter are considered, however, the results are distinctly different from those obtained by SHIRLEY under blue glass. They also differ from the conclusions of POPP, TEODORESCO, and others that blue light inhibits the elongation of stems. If only those lamps are considered which emit light from comparatively narrow regions of the spectrum (blue with filter, combination of blue and green with filter, green with filter, gold, pink with filter, and red without filter), there was a decrease in the length of plants in the order named—from blue to red. These results indicate that, for the visible spectrum, the effectiveness in inhibiting the elongation of stems increases from blue to red. Similar results have been reported by DANGEARD (3), JOHNSTON (7), WITHROW (28), WENT (26), WEINTRAUB and MCALISTER (24), and GOODWIN (5). DANGEARD worked with *Lepidium*, WITHROW with bean, WENT with pea, and JOHNSTON, WEINTRAUB, and MCALISTER, and GOODWIN with the first internodes (mesocotyls) of *Avena*. LANGE (10) and SCHNEIDER (19) have also found that elongation of the first internode of *Avena* is definitely inhibited by irradiation with red light.

GOODWIN (5), JOHNSTON (7), and

WEINTRAUB and MCALISTER (24) all found that the effectiveness of radiation in inhibiting elongation of the first internode of *Avena* increased from the blue to the red end of the visible spectrum but rapidly decreased from about 6600 Å or 6800 Å to the infra-red. GOODWIN also found that the effectiveness at 3650 Å was considerably greater than at 4358 Å. The results of POPP and MCILVAINE (18) on turnip plants also indicate that the effectiveness in limiting elongation and in decreasing the amount of growth substance increased from the violet end of the visible spectrum to the region of about 2350 Å in the ultra-violet. Similar results were obtained by BURKHOLDER and JOHNSTON (2).

It therefore seems probable that the effectiveness of radiation in inhibiting stem elongation may have at least two maxima, one in the ultra-violet and one in the red, and at least two minima, one in the blue region of the visible spectrum and the other in the long red and infra-red. There are some indications, however, that radiation from all parts of the visible spectrum may be even more effective than an equal amount of radiation in the red region.

MCILVAINE and POPP (11) found that turnip seedlings grown under a Mazda lamp with a red filter were shorter than those grown under the same lamp with a green or violet filter. Similar results were obtained with these three filters when daylight was used as the light source. In these cases equal energies were used, but they point out that, because of the considerable amounts of infra-red, the intensity of the radiation from the visible region of the spectrum may not have been equal. These results agree with the generalization just made by the writer, although their other results do not agree so well.

In the experiments of McILVAINE and POPP (11), plants were grown under G34 and G403ED filters made by the Corning Glass Company. Three sources of light were used: a Mazda lamp, a mercury vapor lamp in quartz, and the combined radiation of a Mazda lamp and a mercury vapor lamp in glass. With all three sources, the plants grown under the red end of the spectrum as limited by the G34 filter were taller than those grown under the blue end as limited by the G403ED filter. Equal amounts of energy were applied to the plants from each end of the spectrum. These workers give 5290 to 7200 Å as the spectral range of the G34 filter and 3740 to 5850 Å for the range of the G403ED filter. Apparently these values were intended to pertain only to transmission in the visible spectrum. This is indicated by their reference to "the differences of transmission in the infra-red region" of the red, green, and violet filters for which the upper limit of transmission was listed as 685 m μ . The spectrograms published by SHIRLEY (20) indicate that the G403ED filter transmitted radiation from 3550 to 5850 Å. The G34 filter is known to transmit a considerable amount of infra-red. It seems probable, therefore, that a high percentage of the energy reaching the plants under the G34 filter—when the Mazda lamp was used as the source—was infra-red, which is relatively ineffective in inhibiting stem elongation, and that much of the inhibition of elongation found under the G403ED filter—when the mercury vapor lamps were used in the light source—may have resulted from irradiation with wave lengths shorter than 4000 Å.

As mentioned in the writer's experiments with bean, the lengths of the upper internodes did not follow the same order, as shown by the hypocotyls and first

internodes. There was a tendency for plants with short hypocotyls and first internodes to produce long internodes toward the top of the plant, and for those plants with long hypocotyls and first internodes to produce short internodes toward the top of the plant. This "compensating effect" was noticed by WENT (26) in the case of Alaska peas but not in the case of Little Marvel peas. The amount of food supply may well have been the controlling factor for the upper internodes, since for the most part the plants with the greatest dry weight tended to produce longer internodes at the top of the plants. The relation between food supply and effect of auxin has been discussed by WENT (25).

In general, the effect of light quality on leaf area in these experiments was similar to those noted by WENT (26) for pea plants, but the development of very small leaflets on the plants grown under the red fluorescent tubes does not appear to be in agreement with WENT's observations.

NEMEC and GRACANIN (15) reported that the amount of potassium found in rye plants grown under red and violet glass and in daylight was greater than in plants grown under green glass. The results described in this paper for bean plants do not seem similar. In these experiments no consistent differences were found in the amount of potassium present under the different conditions of light quality, except that the highest values in percentage of ash for the leaves and for the entire tops were found in plants grown under the green tubes without the filter, and the highest values for the stems were found under the blue tubes without the filter. NEMEC and GRACANIN also reported that the amount of phosphorus in the plants grown under the different glasses decreased as follows:

green glass, violet glass, sunlight, and red glass. The phosphorus content of the bean plants grown under the fluorescent tubes was greatest under green and least under light which most nearly resembled white light.

Plants grown under the more balanced radiation of the pink, daylight, and blue tubes without filters were high in leaf area, dry weight, and calcium content but low in phosphorus content; plants grown under the green tubes with the filter were lowest in leaf area, dry weight, and calcium content but highest in phosphorus content. While it would be expected that plants which have small leaves might produce small amounts of dry weight, it is probable that the correlation between these values may be more directly related to light quality than on that basis alone.

Summary

1. Red kidney bean plants were grown under fluorescent lamps of various colors. Dyed gelatin filters were used with some of the lamps to narrow the spectral regions used. The plants under each of the lamps received equal amounts of incident energy as measured with a thermopile.

2. The lengths of the hypocotyls and first internodes were least in the plants receiving light from nearly all parts of the visible spectrum. Light from the daylight and blue tubes produced very little differences in the plants. If only the plants grown under lamps and filters which emitted light from rather narrow regions of the spectrum are considered, the effectiveness in inhibiting elongation was greatest in the red and least in the blue regions.

3. The average leaf area and the production of dry weight were greatest in

the plants receiving the more balanced radiation. If only the plants which received light from rather narrow regions of the spectrum are considered, the average leaf area was least in the green and slightly greater in the red than in the blue. Dry weight production was also least in the green but very nearly equal in the red and blue regions.

4. Visible flower buds developed earlier under green light than under the other lamps, but many of these buds abscised.

5. No significant differences in the amount of total ash, or in the percentage of potassium or magnesium in the ash, were found in the plants grown under the different lamps.

6. The amount of calcium in the leaves, expressed as percentage of ash or of dry weight, was closely correlated with dry weight production and was highest in those plants receiving energy from most of the visible spectrum and lower when narrower regions were used. When the calcium content of the leaves was high, the content of the stems was low, and vice versa.

7. The amounts of phosphorus found in plants grown under the more balanced light of the daylight, pink, and blue tubes without filters were almost equal. It was higher in those plants which received no radiation in the blue and also in those which had received no radiation from the red end of the spectrum. It was still higher when light from both ends was absent.

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